Associations between parasitic blow flies and the breeding density and synchrony of cavity nesting passerines

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Biology Honors Thesis
Appalachian State University
Submitted to the Biology Department in partial fulfillment of the requirement of the degree of Bachelor of Science
May, 2018

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Abstract

Understanding transmission dynamics of parasites can assist in both disease control and conservation. Parasite load is traditionally viewed as a function of host density, but this model fails in some instances, usually depending on the life cycle of the parasite. I examined parasite-host dynamics of two cavity nesting passerines and ectoparasites in the genus *Protocalliphora* using both spatial and temporal parameters. Parasite load was expected to increase with host density. Parasite load was also expected to differ between time intervals. Host density showed no significant influence on parasite load. Parasite load was significantly in early-season nests than in mid-season nests. Parasite load differed significantly between host species, but not between field sites. This study supports the idea that the transmission of parasites with a life cycle in which adults can disperse independently of the host is only loosely related or entirely uncoupled from host density.

Introduction

Parasite-host relationships play a central role in ecosystems, whether the parasite eventually kills its host, acts as a vector, or lowers the host's fitness by degrading the host's body condition or even altering its behavior. Parasites, defined as an organism that lives in or on a host organism for all or part of its lifecycle to the detriment of the host, can include viruses, bacteria, protozoa, fungi, plants and animals. The life history of the parasite influences both mode of transmission and the evolutionary trajectory of the parasite-host relationship. Here, I investigate the transmission dynamics of blow fly ectoparasites (*Protocalliphora)* in relation to nesting synchrony and density of two host species (*Sialia sialis* and *Tachycineta bicolor)*.

In 1911, Ronald Ross developed a model to simulate the transmission of malaria across a population. In this model, the determination of the reproductive rate of the parasite can either depend on the density of the host or vector, or on the prevalence of infected hosts in a population (Dietz 1988). The importance of host density in predicting parasite load depends on mechanisms of parasite dispersal and transmission from host to host, making the predictions highly species-dependent. If the chance of a host coming into contact with a parasite in its transmission stage increases with host density, then host density should be positively correlated with parasite load. Parasite-host population dynamics are further complicated by the potential ability of parasites, among other environmental factors, to put constraints on the population density of the host species.

Anderson and May (1978) modelled the relationship between host species and Eucaryotic macroparasites. Their model assumes (1) that the parasite does not kill its host as a prerequisite for its own development or survival, (2) that birth and death rates of the host are altered by the

parasites they harbor, and (3) that if the parasite fails to control the host population, the host population will experience exponential growth until resource limitation slows growth. This model is similar to the Lotka-Volterra equations, producing population numbers of both parasite and host species that oscillate over time in response to each other's influence. The introduction of parasite density was shown to have a stabilizing effect on the model.

In general, host density is positively correlated with infection of parasites (Bradley 1972), especially in the case of microparasite infection. When considering microparasites, hosts can be classified as infected, not infected, or recovered. However, with macroparasites, parasite load or the number of parasites infecting a host organism must also be considered as a factor influencing transmission dynamics (May & Anderson 1990). One model (Dobson 1990) showed a positive relationship between host density and parasite abundance. Parasite abundance incorporates both prevalence (proportion of host population infected) and intensity (mean number of parasites per infected host). A meta-analysis on mammalian nematodes found a strong correlation between parasite density and host population density among closely related mammal taxa or when controlling for host body size across species (Arneberg et al. 1998).

In theory, virulence, or the parasite-induced death rate of the host, should be reduced over a period of coevolution to the benefit of the parasites because it would allow hosts to be parasitized for longer periods of time. This hypothesis is inconsistent across a range of parasites, including the rabies virus and many species of parasitic wasp, whose reproductive cycles are dependent on killing the host organism (Anderson & May 1982, Toft & Karter 1990). Evidence suggests that the life history of the parasite determines whether that parasite benefits or is harmed by the death of its host (Clayton & Tompkins 1994). Blow fly parasitism of songbirds has been shown to cause anemia in parasitized chicks (Hannam 2006, O'Brien et al. 2001,

Hurtrez-Bousses 1997) and in some cases lower body condition (Hurtrez-Bousses 1997) and higher mortality (Merino & Potti 1995). Other studies found no significant effects on the fitness of songbird nestlings (Roby et al. 1992, Hannam 2006).

Here, I test the hypothesis that there is a relationship between blow fly infestation and breeding density of two breeding box nesting passerines: eastern bluebirds (*Sialia sialis*) and tree swallows (*Tachycineta bicolor*). I predicted that breeding density would increase with parasite load. I expected that parasite load would decrease with mean distance between avian neighbors and with increasing distance to nearest avian neighbor. Because blow flies are thought to lay eggs in nests with host nestlings present, I expected that the timing of nest activity would affect nest parasite load, with mean parasite load increasing in uniformity within time intervals and differing significantly between time intervals.

Methods

Study Species

Tree swallows and eastern bluebirds are both obligate secondary cavity nesters, so breeding density is to some degree limited by availability of nest cavities. Both species prefer open field and pasture habitat, successfully breeding in disturbed habitats like agricultural lands, pastures, fields and golf courses (Stanback & Seifert 2005). Eastern bluebirds occupy a foraging range of approximately 3.6-8 hectares (Pinkowski 1977). Tree swallows are considered loosely colonial, tend to nest at higher densities than bluebirds and have a typical foraging range of 100-200 m from the nest (McCarty & Winkler 1999). In the past century, eastern bluebirds experienced a sharp population decrease due to a number of possible factors including: competition from invasive species, habitat loss, and pesticide use, but have largely recovered

over the past few decades. Tree swallows, historically distributed over much of northeastern North America, are experiencing a range expansion southward (Duckworth 2008).

The blow flies most commonly observed parasitizing both eastern bluebird and tree swallow nests are two similar species: *Protocalliphora sialia* and *P. occidentalis* (Whitworth 2003). Once hatched, blow fly larvae experience a period of active feeding before transitioning into a post-feeding larval form and finally forming a puparium. Many species of blow fly disperse to a location suitable to burrow and pupate after feeding (Gomes et al. 2006). Post-feeding larval dispersal is not considered a factor in this study because the blow fly species that parasitize cavity nesting birds tend to pupate in the nest cavity and emerge as adults, which is when dispersal begins. This first stage of development has been documented as lasting 7-9 days in *P. sialia* (Bennett & Whitworth 1991). Adult females can live up to 170 days with an average lifespan of 76 days. Females typically lay about 100 eggs within 1-2 weeks of emergence and are assumed to oviposit only in bird nests with nestlings present. MacLeod & Donnelly (1960) concluded that the zone of influence of several blow fly species was approximately 4 hectares around the spot where individuals were released, and individuals have been documented crossing an expanse of water 90 m across. The radius of a circle 4 hectares in area is approximately 113.5 m, so a buffer zone of 114 m around each infested nest was included in statistical analyses.

Field Methods

During the 2017 breeding season, I monitored 300 nest boxes at two field sites in Watauga County, North Carolina. These nests have been monitored by Dr. L. Siefferman since 2009. Both sites are rural areas, with sparse buildings and large portions of open pastures and fields. Most nestboxes are used either by tree swallows or eastern bluebirds, however the Meat Camp site has a relatively even distribution of tree swallows and bluebirds while Valle Crucis is

dominated by tree swallows. At both sites, some boxes are also used by house wrens (*Troglodytes aedon*), Carolina chickadees (*Poecile carolinensis*) and house sparrows (*Passer domesticus*). Meat camp was the larger of the two sites, with boxes distributed across an area of ~ 6,300 hectares. Valle Crucis nest boxes are more clumped in distribution, in an area of ~ 900 hectares.

Each year, at the end of the breeding seasons, field workers remove old nest material from boxes. I monitored all nest boxes during the breeding season and recorded the number of eggs, nestlings, and fledglings. I considered nests 'active' if at least one egg was laid. I recorded whether the eggs hatched and determined whether nests were predated, nestlings died in the nests, and assumed they fledged if nestlings were absent from nests during the expected fledging stage. I captured and banded adults (female tree swallows and both sexes of bluebirds) at the box during incubation or nestling rearing. Nestling bluebirds and tree swallows were briefly (~5 min) removed from the nest at ages 8 and 14 days post hatch for banding and recording of body mass. I noted the presence of any parasite attached to nestlings. After nestlings had fledged, I collected a random selection of 70 nests from bluebirds and tree swallows (Table 1). Nests were held in a -20° freezer until nests were carefully searched for blow fly puparia/adults. Flies of all life history stages were counted and recorded. Parasite load is defined as the total number of *Protocalliphora* divided by the number of nestlings per nest.

Spatial Analysis

Bluebird and tree swallow nests were included in spatial analyses if nestlings reached at least 4 days old. I used the point distance tool in ArcMap to calculate the distance between each infested nest and the active nests within a 300m radius of the focal nest. I preformed statistics on

two groups separately: a group with all active neighbors within a 300 m buffer of the focal nest and group with all active neighbors within a 114 m buffer of the focal nest.

Statistical Analyses

Parasite load was not normally distributed, so nonparametric tests were used to analyze relationships. I used Mann-Whitney U Tests to compare means of parasite load between the two field sites (Valle Crucis and Meat Camp) and to compare parasite loads between eastern bluebirds and tree swallows. I used Spearman's correlation to analyze the relationship between parasite load (represented as total parasites/ brood size) and number of neighbors, mean distance to neighbor, and distance to closest neighbor using both 114m and 300m buffers. I used one-way ANOVAs and Turkey post-hocs to analyze the difference between means of three groups of nests: early, mid, and late season nesters. Early nesters were categorized as all nests that hatched chicks before May 19th, mid-season nesters hatched between May 19th and June 3rd, and late nesters hatched after June 3rd. All collected nests hatched and fledged between April 18th and June 30th. Nests were further broken down by site, creating five groups (mid- and late-season nesters in Valley Crucis and early-, mid-, and late-season nesters in Meat Camp), which were also analyzed using one-way ANOVA and Turkey post-hoc tests. SPSS V24 was used for all statistical analyses.

Results

Species and Site

A total of 257 bluebird and tree swallow nests were active over the course of the breeding season, including 227 nests with nestlings that had reached at least 4 days old (Table 1). Additionally, 30 nestboxes were used by non-target songbird species; 11 Carolina chickadee, 18

house wrens and 1 house sparrow nests. Overall, 76.9% of bluebird nests and 86.7% of tree swallow nests were parasitized by the ectoparasite *Protocalliphora* sp. Moreover, 80.0% of Valle Crucis and 81.8% of Meat Camp nests were parasitized. Of the nests collected, 81.2% were parasitized.

Tree swallow nests were more densely distributed than bluebird nests (Fig. 1 & Fig. 2). Birds nested in higher density at the Valle Crucis site compared to the Meat Camp site (Table 2). Mean parasite load was not significantly different between sites (n=69, P=0.102, U=379.0, Z=-1.636; Fig. 3). Mean parasite load was significantly higher in eastern bluebird nests compared to tree swallow nests (n=69, P=0.010, U=372.0, Z=-2.581; Fig. 4).

Density

There was no significant relationship between parasite load and number of neighbors within 300m (n=69, P=0.644, r=-0.057; Fig. 5) or within 114m (n=69, P=0.794, r=0.032; Fig. 6). There also was no significant relationship between parasite load and mean distance to neighbors within 300m (n=68, P=0.895, r=-0.016; Fig. 7) or within 114m (n=55, P=0.342, r=0.130; Fig. 8). There was no significant relationship between parasite load and distance to nearest neighbor within 300m (n=68, P=0.506, r=0.082; Fig. 9) or within 114m (n=55, P=0.838, r=0.028; Fig. 10).

Time intervals

All early nesters were eastern bluebirds nesting in the Meat Camp site. Mid-season nesters were composed of 11 bluebird nests (4 in Valley Crucis, 7 in Meat Camp) and 20 tree swallow nests (14 in Valley Crucis, 6 in Meat Camp). In the late nesting group, there were 18

bluebird nests (4 in Valley Crucis, 14 in Meat Camp) and 9 tree swallow nests (3 in Valley Crucis, 6 in Meat Camp).

When both sites were combined, parasite load differed significantly between time intervals (df=68, F=7.912, P=0.001; Fig. 11). Parasite load was significantly higher in early nesters compared to both mid-season nests (P=0.001) and late-season nests (P=0.009) but mid-season and late-season nests did not differ significantly (P=0.524).

When data where split by field site, parasite load also differed significantly by time intervals and field site (df=68, F=3.650, P=0.010; Fig. 12). Early season nests at Meat Camp had significantly higher parasite load compared to mid-season nests at Valle Crucis (P=0.004). But early season nests at Meat Camp did not differ significantly in parasite load from mid-season nests at Meat Camp (P=0.061), or with late season nests at Valle Crucis (P=0.191), and were only marginally higher in parasite load than late season nests at Meat Camp (P=0.051). Mid-season Valle Crucis nests were not significantly different in parasite load from mid-season nests at Meat Camp (P=0.908), late season nests at Valle Crucis (P=0.924), or late season nests at Meat Camp (P=0.766). Parasite load at mid-season nests at Meat Camp were not significantly different from late season nests at Valley Crucis (P=1.000) or late season nests at Meat Camp (P=1.000). Late season nests at Meat Camp did not vary in parasite load from late season nests at Valley Crucis (P=1.000).

Discussion

I found that bluebirds experienced a higher parasite load than tree swallows but that parasite load did not vary with field site and birds bred at higher density at the Valle Crucis site compared to the Meat Camp field site. Moreover, I found no evidence that parasite load varied

with breeding bird density. However, I did find evidence of temporal patterns of parasite abundance; parasite abundance was higher in the early and late breeding season compared to the mid breeding season. Bluebird initiated nests earlier than tree swallows and also have a longer breeding season because they are double brooded while swallows are single brooded. These temporal patterns probably reflect the timing of higher bluebird and tree swallow nesting. Finally, contrary to many parasite studies, I found no evidence that parasite load varied with bird breeding density. The blow fly species at my field sites is most likely *Protocalliphora sialia* or *P. occidentalis* as both parasitize these bird species and occur in eastern North America.

My data do not support the hypothesis that avian breeding density is associated with blow fly parasite load. Both the dispersal habits of the parasites and host behavior could account for the absence of a strong relationship. True relationships could also have been difficult to detect due to small sample size, and an incomplete picture of parasite load across all active nests, including other potential hosts (house wrens, Carolina chickadees, and nearby cup-nesting species). *Protocalliphora sialia* has been known to parasitize a range of other species, including house wrens, without exhibiting high amounts of host preference (Bennett & Whitworth 1992). Although a small percentage (11.7%) of nestboxes were used by species other than bluebirds and tree swallows, I did not collect their nests and this is a limitation of my study design.

My results are not consistent with other avian studies which found that birds breeding in higher densities experience higher ectoparasite loads. A study of lice in populations of colonial bee-eaters found that inter-nest distance and colony size were the best predictors of parasite load (Hoi et al. 1997). As a colonial breeder, bee-eaters live in very high densities and therefore come into contact with conspecifics more often than bluebirds or tree swallows. This discrepancy may result from species differences in group size and distance between neighbors. Tree swallows are

considered semi-colonial and generally breed in a more clustered distribution than eastern bluebirds. My data revealed however that tree swallows experienced significantly lower parasite loads than the bluebirds. It is likely, though, that higher parasite loads in bluebirds is a consequence of the parasites' higher affinity for bluebird hosts compared to tree swallows. Species level identification of the parasite would shed light on these patterns and help separate the potential confounding factor of host specificity versus temporal patterns in parasite abundance.

Many studies of parasite transmission examine host sociability on the assumption that higher instances of host conspecific interactions aid in the spread of parasites from host to host. Studies of social species generally conclude that parasite load increases with host density (Krasnov et al. 2002, Godfrey et al. 2009, Bordes et al. 2007, Rimbach et al. 2015). In contrast, in high density-living lizards, parasite load is negatively correlated with density (Sorci et al. 1997). Finally, the extent to which density predicts parasitism depends on the life history characteristics of two parasites when compared in the same study (Whiteman & Parker 2004). I did not consider conspecific interactions in this study because adult blow flies can disperse freely while larvae only take blood from nestlings. Nestlings only come into contact with siblings within the same nest, making transmission via the host unlikely. Previous studies indicate that solitary nesters are more often parasitized by ectoparasites with flying adult forms (Loye & Carroll 1995). In fact, dispersal efficiency (flight distance) may be functionally necessary to parasitize solitary nesters because the hosts so rarely come into contact with conspecifics.

The possibility that blow fly dispersal and host selection is influenced by a variety of environmental factors is worth exploring. Research from the blow fly perspective is lacking, but there is evidence that surrounding habitat type can influence blow fly abundance. Although

Remes & Krist (2005) found that blow flies are more common in European oak-dominated than spruce-dominated forests, Wesolowski (2006) found that forest type did not predict parasite load. Moreover, some species of *Protocalliphora* show strong host preferences while others show strong site preferences (Bennett & Whitworth 1992). Future research should investigate whether land use surrounding active bluebird and tree swallow nests predicts *Protocalliphora* parasite load.

My data yielded some support for the hypothesis that parasite load is related to time constraints; early nests were most heavily parasitized and mid-season nests had the lowest parasite load. The difference in parasite load over time could be the consequence of a number of factors, including: weather patterns and breeding synchrony of neighboring hosts. Experimental manipulation of temperature has been shown to influence blow fly populations in bird nests (Dawson et al. 2004) indicating that fluctuations in weather over the course of the season could explain variation in parasite load. Differences in parasite load may also be attributed to differences in temporal patterns of the breeding seasons of eastern bluebirds and tree swallows. Bluebirds breed earlier in the season and can produce two successful broods while tree swallows initiate breeding a few weeks after bluebirds and produce only one successful nest per season. If these species of *Protocalliphora* prefer bluebird hosts, as the data suggests, then parasites should be more abundant in the earlier part of the season, which is dominated by bluebirds.

The results of this study indicate that the life history traits of parasites are perhaps the most important factors when determining patterns of transmission. The assumption that host density will influence the spread of parasites is based on either direct or indirect contact (ie asynchronous use of the same nest box) with conspecifics being the main mode of transmission. When considering a parasite that disperses independent of the host during part of its life cycle

and can live for days or even weeks before finding a host and reproducing, host density becomes less important than understanding how the parasite selects new hosts, if it is at all selective, and how dispersal is influenced by environment. I conclude, that when studying transmission of parasites that do not rely on contact between hosts for transmission, more attention must be turned to parasite behavior and distribution than that of the host. My results must be interpreted with caution however, as this was a preliminary study to understand spatial and temporal patterns of *Protocalliphora* parasitism on secondary cavity nesting passerines in the Southern Appalachian Mountains.

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Tables

Site	Species	Active Nests	Nests with Nestlings	Nests Collected
MC	EABL	98	78	32
MC	TRES	50	31	12
VC	EABL	27	22	7
VC	TRES	52	36	18

Table 1. Summary of active nests and nests collected in Meat Camp (MC) and Valle Crucis (VC) North Carolina from eastern bluebirds (EABL), tree swallows (TRES).

Site	Species	Avg. Dist. (m)	Max Dist. (m)	Min Dist. (m)
MC	TRES	2,970.9	7,860.7	138.6
VC	TRES	1,376.5	3,031.2	27.5
MC	EABL	2,688.3	8215.7	58.2
VC	EABL	1,883.3	3,196.0	223.0

Table 2. Summary of distance between nests with nestlings. Data includes both eastern bluebirds (EABL) and tree swallows (TRES) in Meat Camp (MC) and Valle Crucis (VC) sites, NC.

Figures

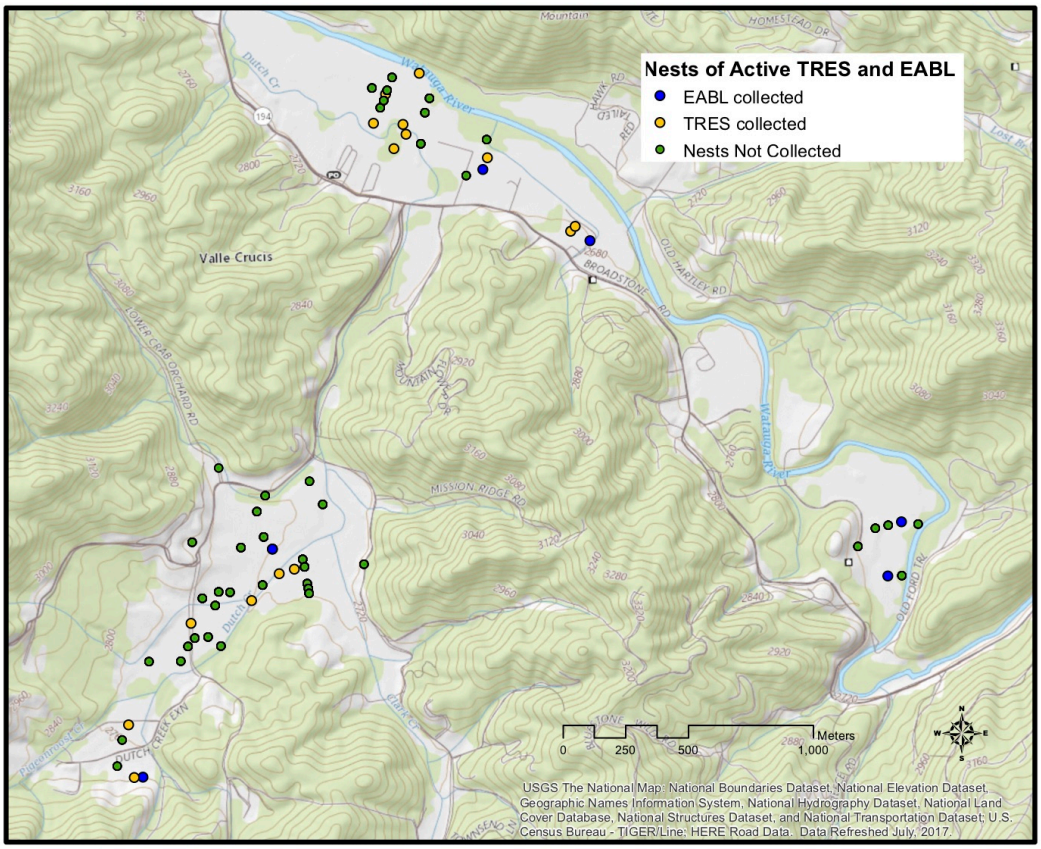

Fig. 1. Map of active tree swallow and eastern bluebird nests in Valle Crucis, NC. All active nests, and those nests that were and were not collected are delineated.

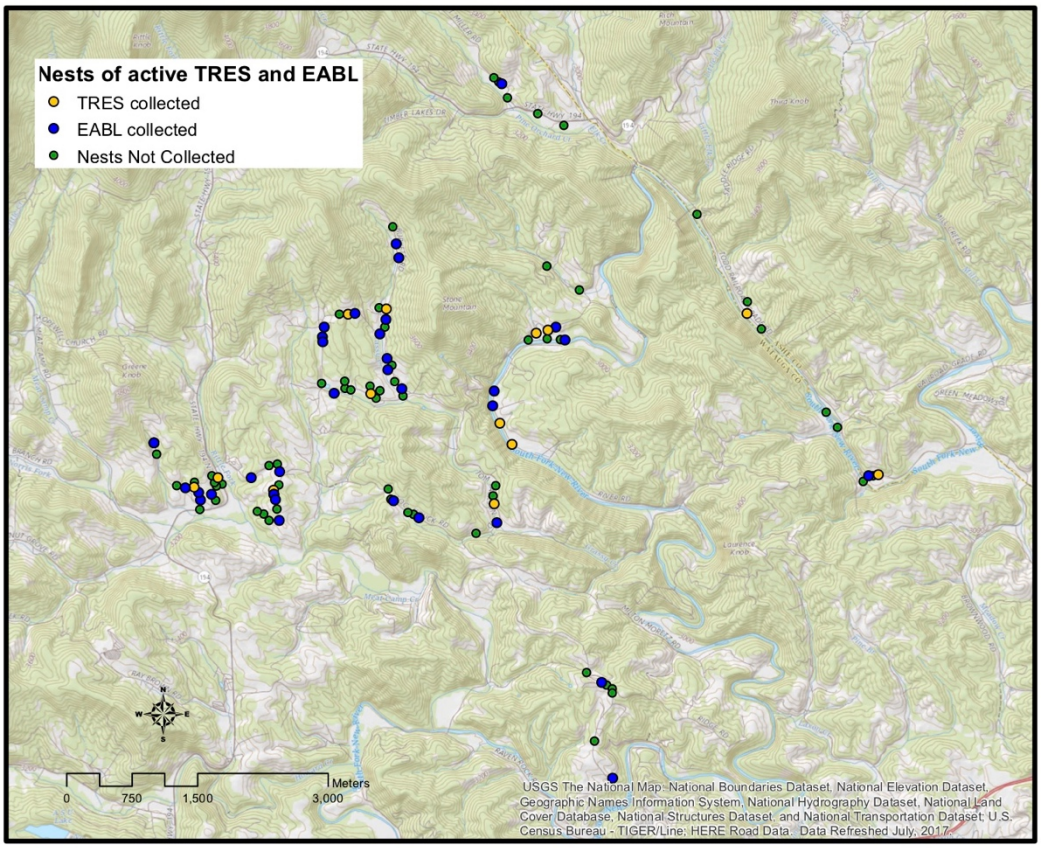

Fig. 2. Map of tree swallow and eastern bluebird nests in Meat Camp, NC. All active nests, and those nests that were and were not collected are delineated.

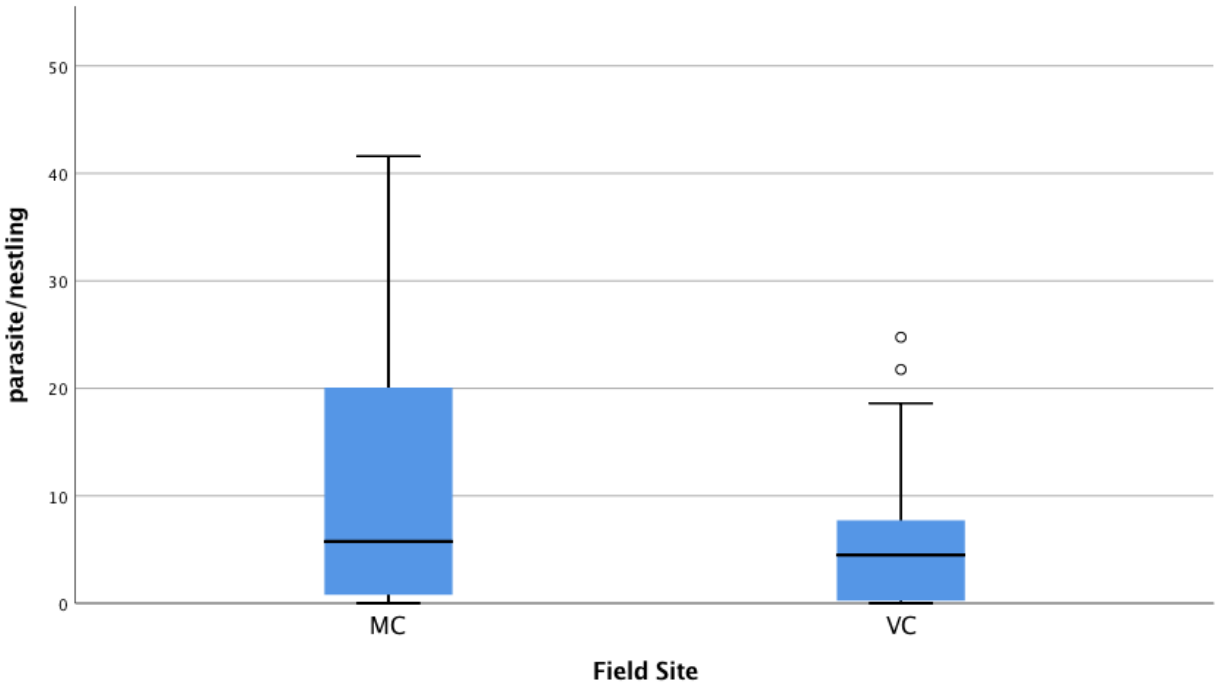

Fig. 3. Comparison of the parasitic load (parasites/nestling) of nests in Meat Camp (MC) and Valle Crucis (VC) field sites, NC. The difference in means was non-significant. Data include both eastern bluebird and tree swallow nests. The boxes represent the 25th and 75th percentiles, the whiskers represent the 10th and 90th percentiles and the line in the box is the median.

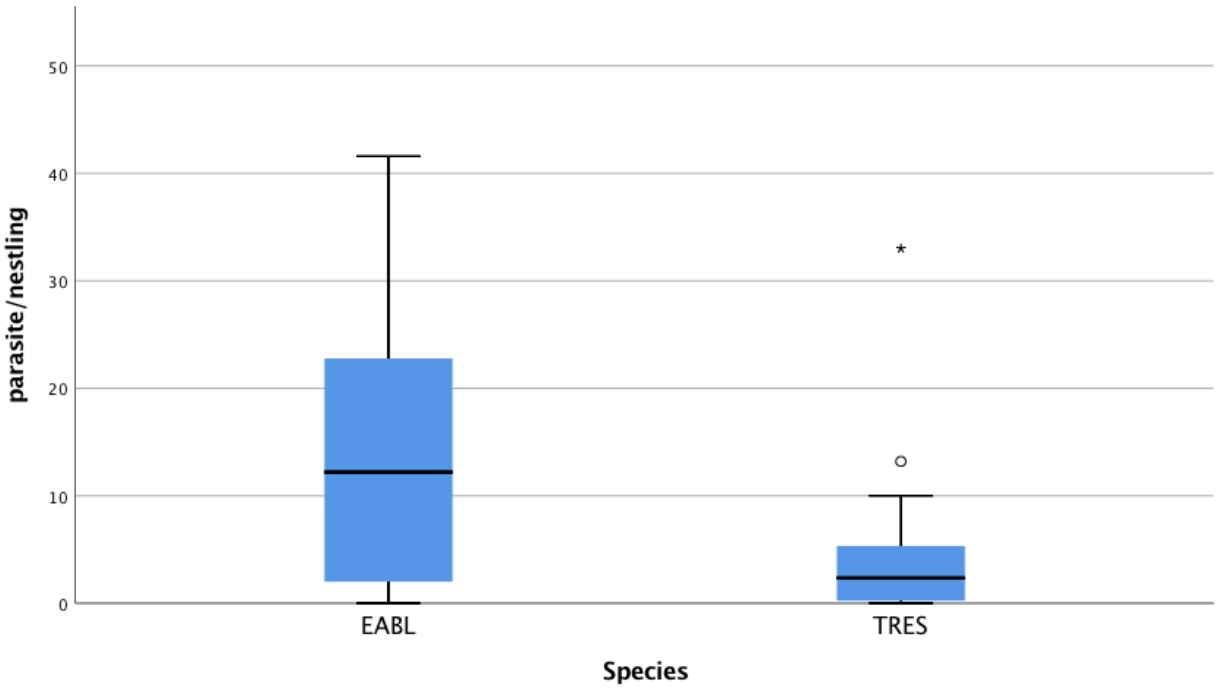

Fig. 4. Comparison of the parasitic load (parasites/nestling) of eastern bluebird (EABL) and tree swallow (TRES) nests. Parasite load was significantly higher in bluebird nests than in tree swallow nests. Data include the Meat Camp and Valle Crucis, NC field sites combined. The boxes represent the 25th and 75th percentiles, the whiskers represent the 10th and 90th percentiles and the line in the box is the median.

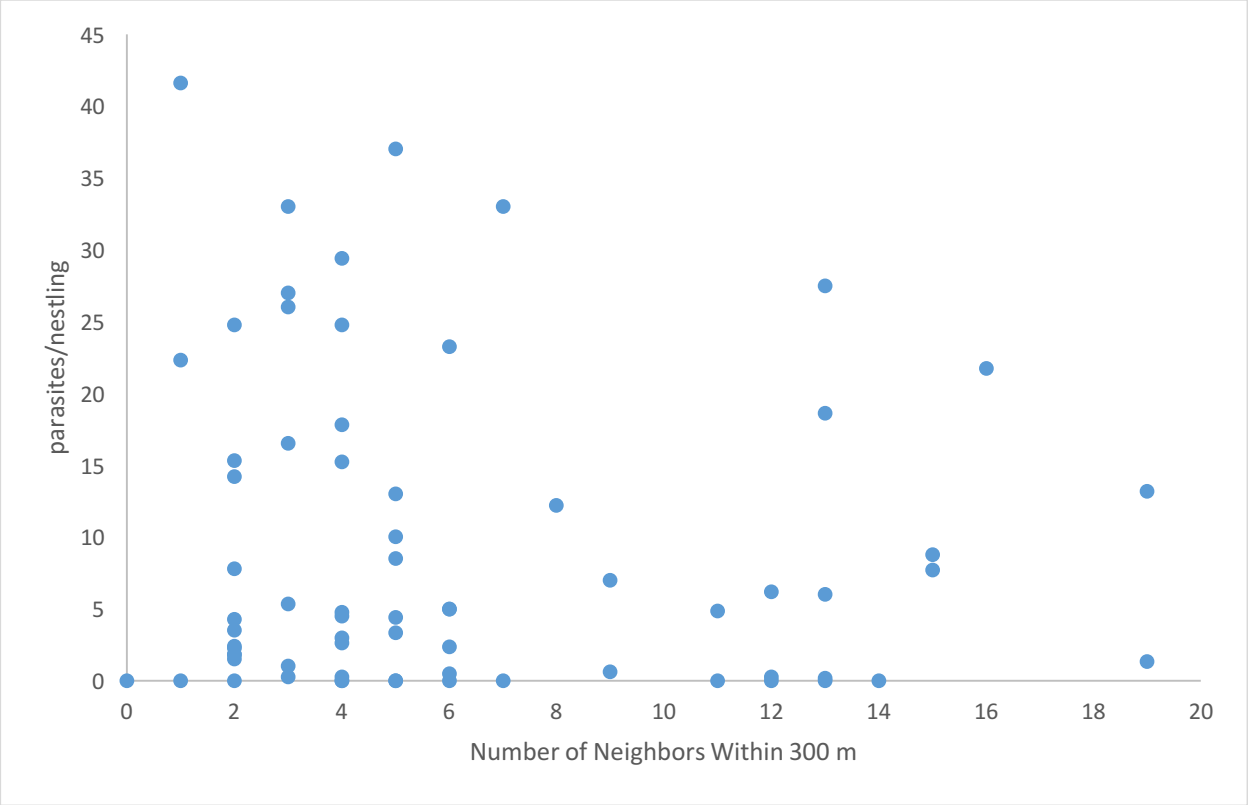

Fig. 5. Relationship between nest density (number of neighbors within 300 m) of breeding birds and parasite load (parasites per nestling). Data includes both field sites and both species. The relationship was non significant.

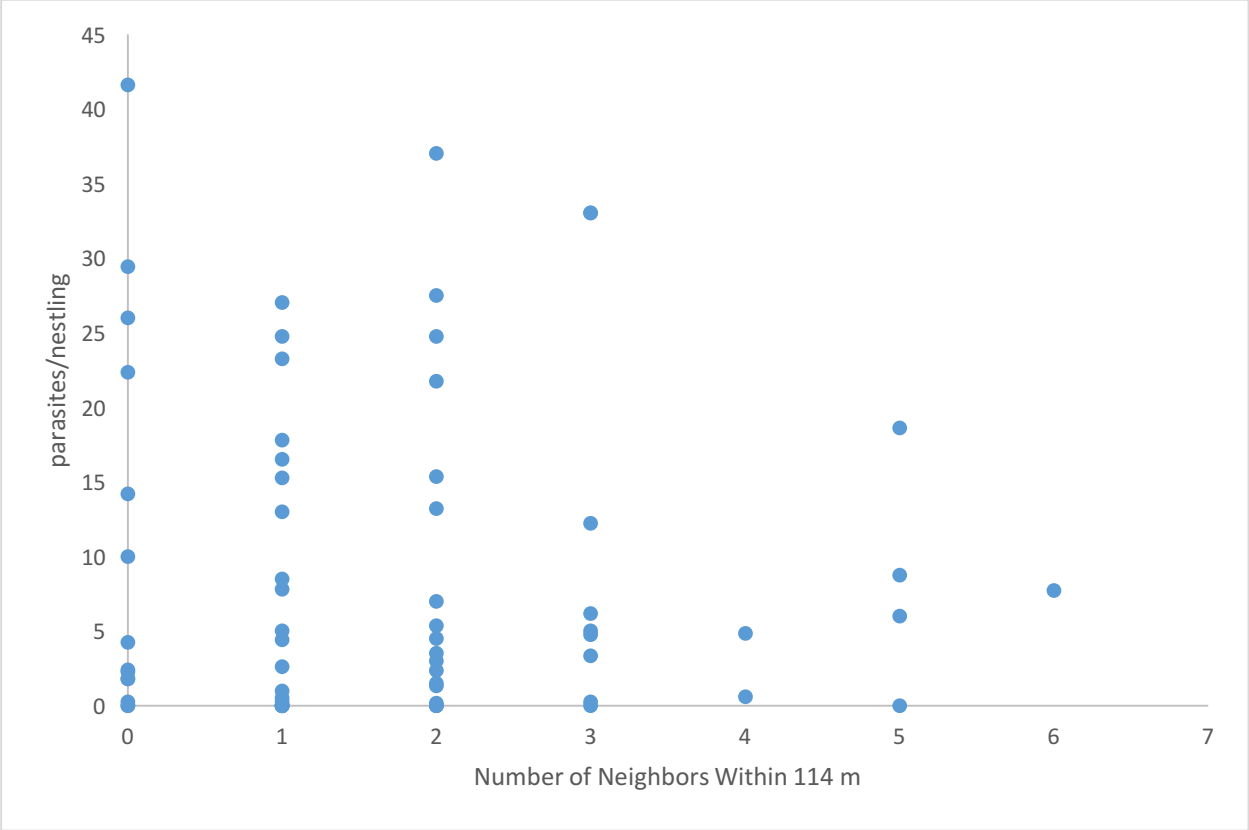

Fig. 6. Relationship between nests density (number of neighbors within 114 m) of breeding birds and parasite load (parasites per nestling). Data includes both field sites and both species. The relationship was non significant.

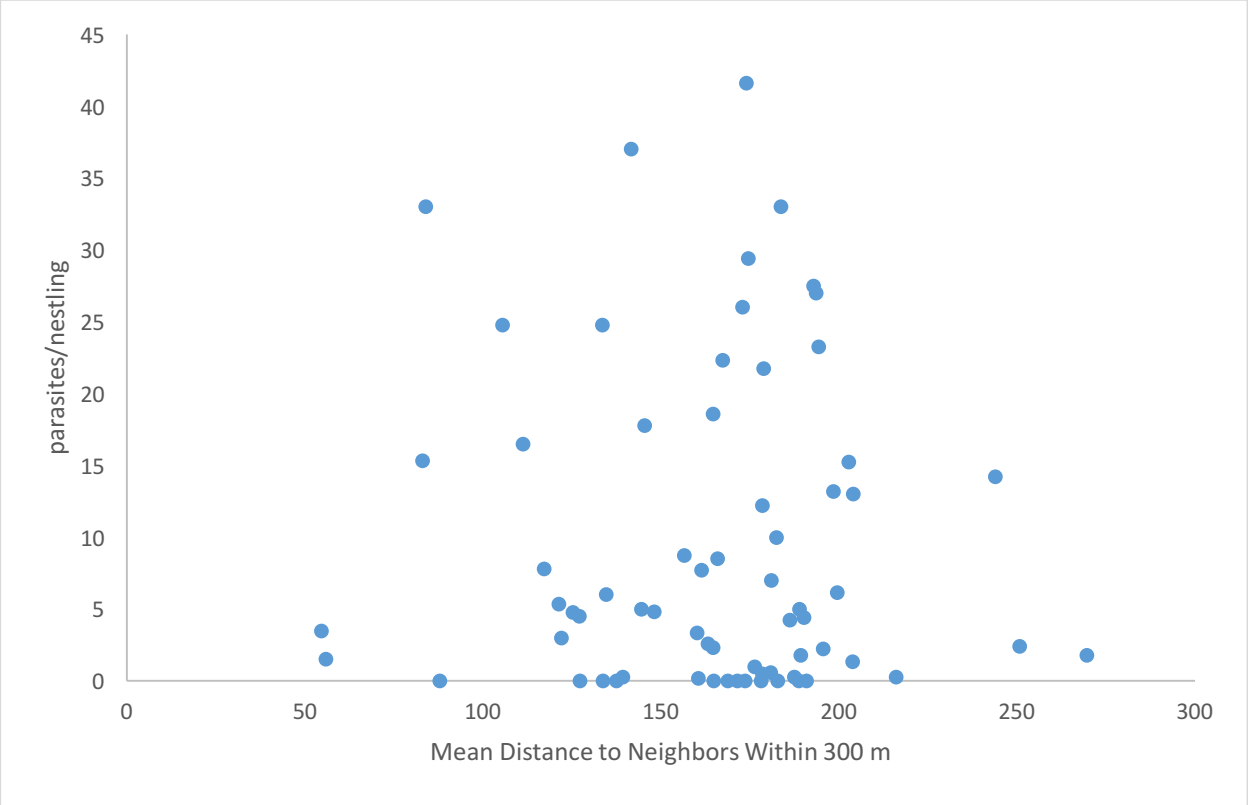

Fig. 7. Relationship between nest density (mean distance to neighbors within 300 m) of breeding birds and parasite load (parasites per nestling). Data includes both field sites and both species. The relationship was non significant.

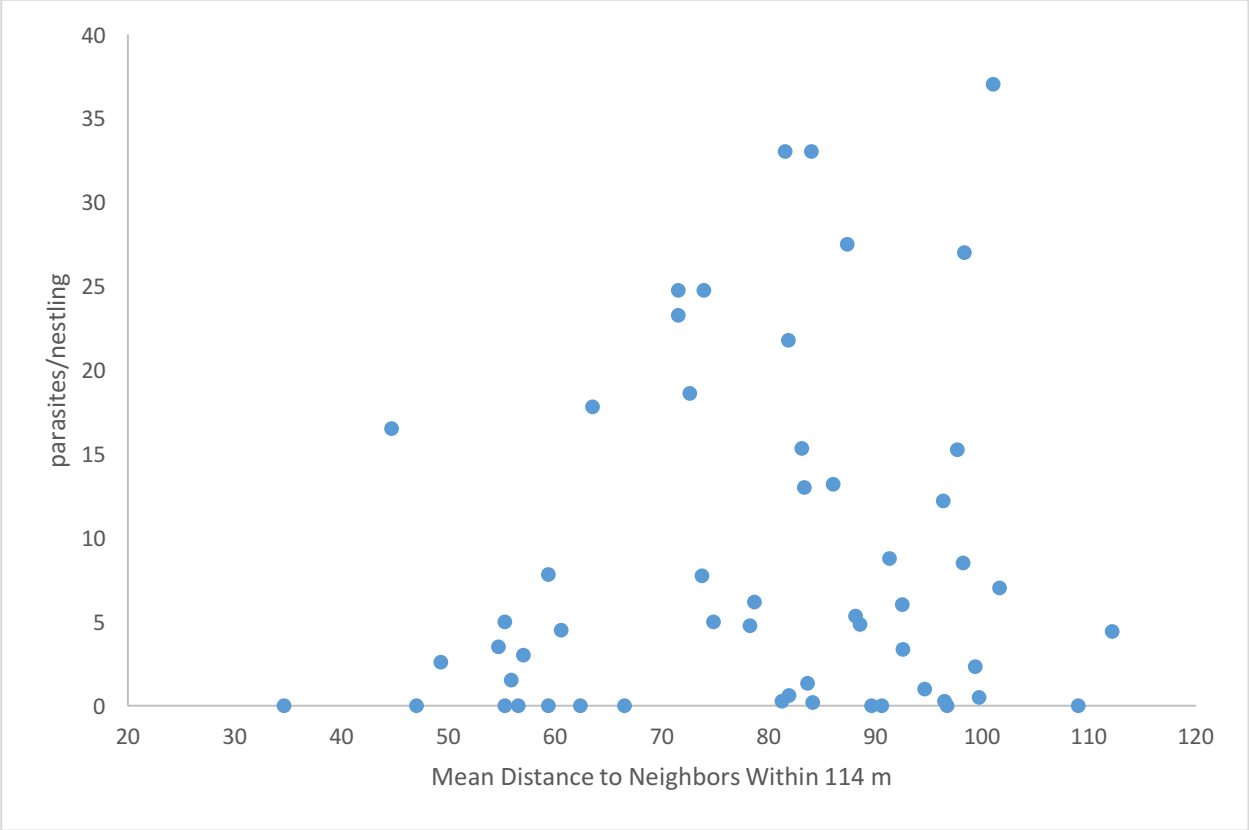

Fig. 8. Relationship between nest density (mean distance to neighbors within 114 m) of breeding birds and parasite load (parasites per nestling). Data includes both field sites and both species. The relationship was non significant.

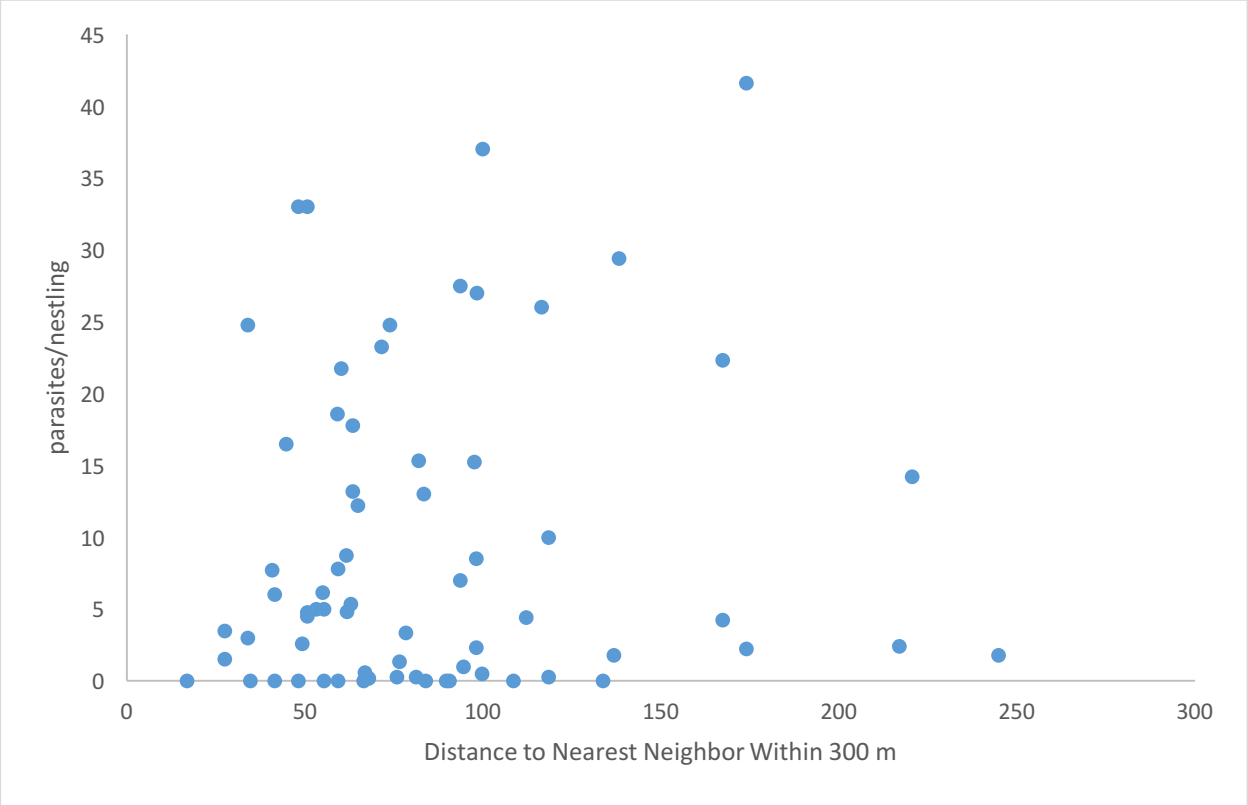

Fig. 9. Relationship between parasite load (parasites per nestling) and distance to nearest neighbor within 114 m. Data includes both field sites and both species. The relationship was non significant.

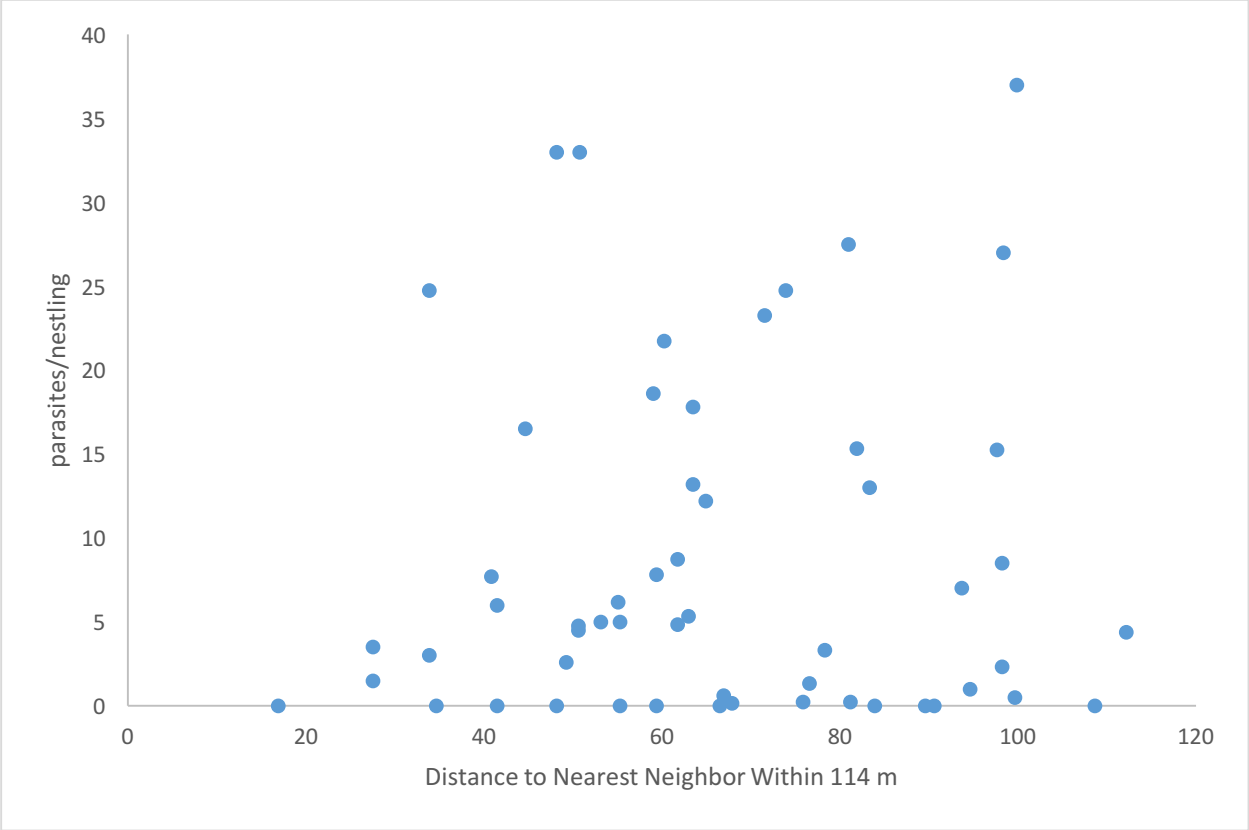

Fig. 10. Relationship between parasite load (parasites per nestling) and distance to nearest neighbor within 114 m. Data includes both field sites and both species. The relationship was non significant.

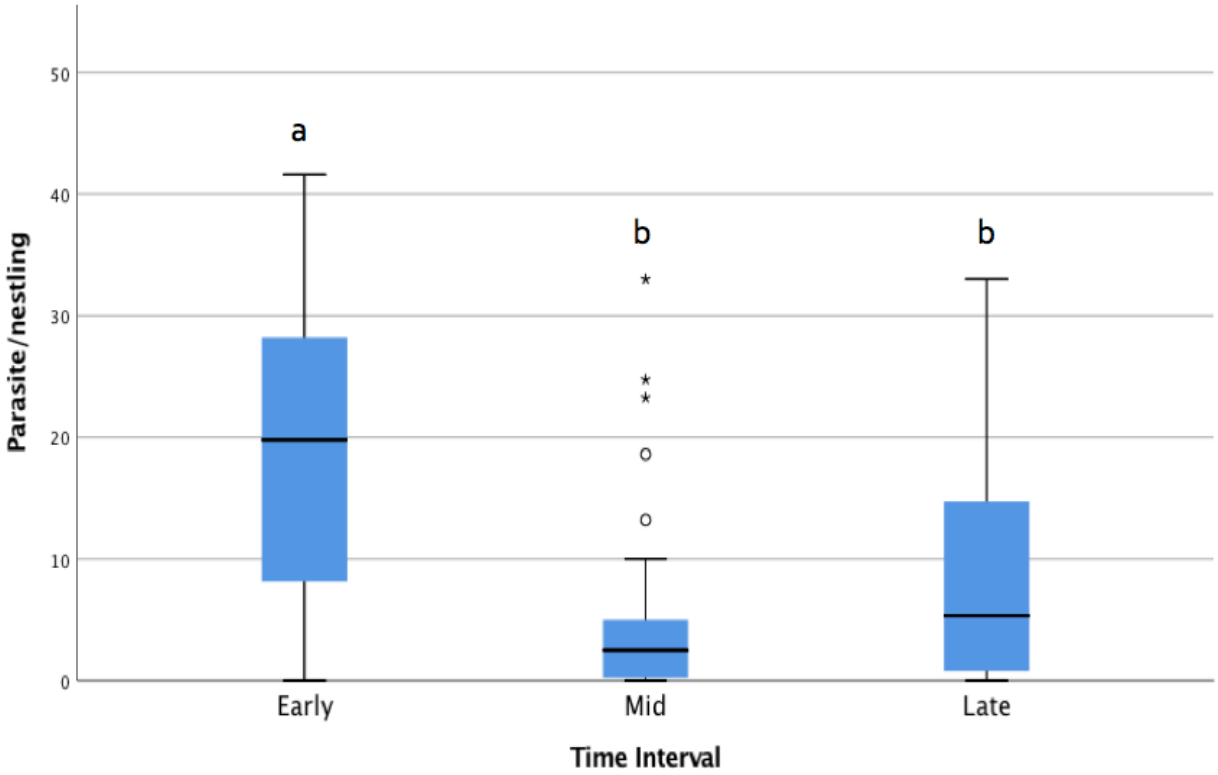

Fig. 11. Comparison of the parasite load (parasites/nestling) of early-, mid-, and late-season nests. Data includes both field sites and species combined. The boxes represent the 25th and 75th percentiles, the whiskers represent the 10th and 90th percentiles and the line in the box is the median.

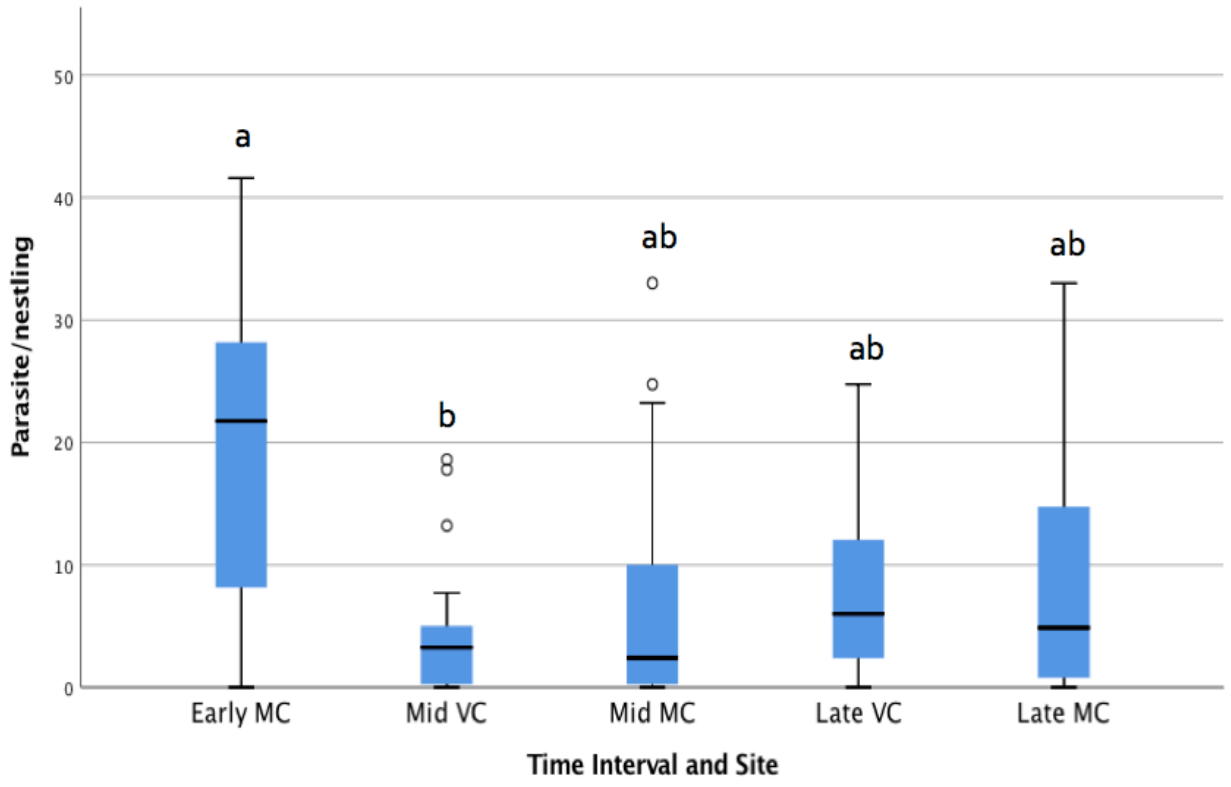

Fig. 12. Comparison of the parasite load (parasites/nestling) of early-season Meat Camp nests (Early MC), mid-season Valle Crucis (Mid VC) and Meat Camp (Mid MC) nests, and late-season Valle Crucis (Late VC) and Meat Camp (Late MC) nests. Data includes both field sites and species combined. The boxes represent the 25th and 75th percentiles, the whiskers represent the 10th and 90th percentiles and the line in the box is the median.